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Air Pockets: A Subtidal Habitat for the Intertidal Marine Pulmonate Limpet *Trimusculus reticulatus*

by

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Abstract. Subtidal air pockets were found to serve as a unique habitat for the intertidal pulmonate limpet *Trimusculus reticulatus*. Observations indicated that the bubbles, discovered on the underside of a ledge approximately 3.5 m deep, arise naturally from air suspended by wave action at high tide. The air-breathing limpets remain sedentary and feed at irregular intervals when the volume of the bubbles decreases sufficiently to immerse them.

INTRODUCTION

During SCUBA diving trips to the reefs of Laguna Beach, California, I noticed pockets of air trapped beneath rock ledges. In subsequent surveys, I found air-breathing limpets of the species *Trimusculus reticulatus* (Sowerby, 1835) occupying many of the bubbles. To my knowledge, there have been no prior studies of such pockets, or of organisms living in this unique microhabitat.

RICE (1985), BEEMAN & WILLIAMS (1980), and YONGE (1958) reported that *Trimusculus reticulatus* is found in the intertidal zone along the west coast of North America. The limpet, which can breathe in air and under water, usually lives clustered in dense colonies on the roofs of caves. WALSBY (1975) showed that, although it retains the ability to move in unnatural situations, *Trimusculus* is essentially sessile. The animal feeds while remaining stationary by secreting a mucus net in which it traps water-borne particles.

Subtidal air pockets, although previously noticed by divers, have not been investigated from an ecological point of view. This study examines the origins of the air pockets and how they serve as a subtidal habitat for a normally intertidal pulmonate limpet.

STUDY SITE

Observations were made in a surge channel that cuts through a rock reef at Shaw's Cove in Laguna Beach, California (33°33′N, 117°48′W). The average depth of the channel is 15 feet (4.5 m), and the width varies from 0.75 m at the narrowest to approximately 4 m at the broadest. At low tide the channel is protected from direct wave action by an outer reef, but at high tide the reef is inundated by 0.3 to 0.6 m of water. The resulting turbulence fills the channel with air bubbles, often all the way to the bottom. The current from a turbulent intersecting cross-channel augments this aeration (Figure 1).

The ledge where the air pockets are found is directly beneath the narrowest part of the main channel and is a result of dramatic widening near the bottom (Figure 2). This overhang is at an average depth of 11 feet (3.4 m). It is approximately 2 m long from its edge to its furthest recesses and 0.5 to 0.75 m above the floor of the channel.

MATERIALS AND METHODS

Observations were made between 5 March and 10 April 1988, by snorkeling, so that the air bubbles were not affected. Depths were measured to the nearest foot using a Dacor depth gauge. The volume of a pocket was measured underwater by removing the air from the cavity with a syringe and emptying it into an inverted graduated cylinder, thus displacing the water. After the volume was read, the air was carefully returned to its original location so that the sampling was relatively non-destructive. Values reported are the volumes of air measured at the depth of the pocket, not at the surface.

To determine whether the bubbles received a significant contribution from the exhalations of SCUBA divers, gas chromatography was performed using a Varian aerograph, model 90-P, using a Porapak column. Air was transferred from a pocket to a sample tube using a 10-mL syringe. Purity of air samples was ensured by performing the transfer completely beneath the surface of the water.

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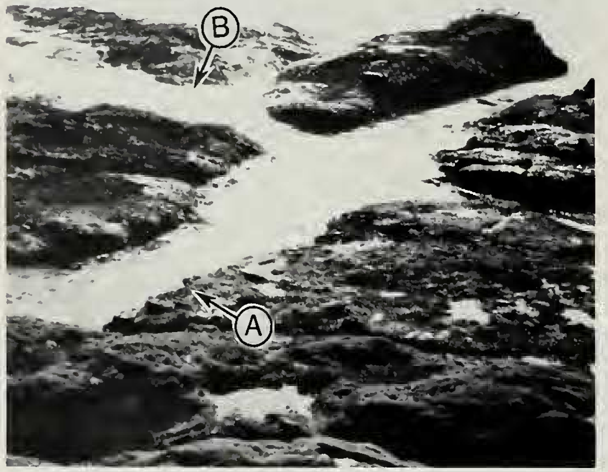

Figure 1

The channel at a +1 foot (+0.3 m) tide. A. The narrowest part of the channel where the cross-section shown in Figure 2 is taken. B. The intersecting channel that provides air to the main channel.

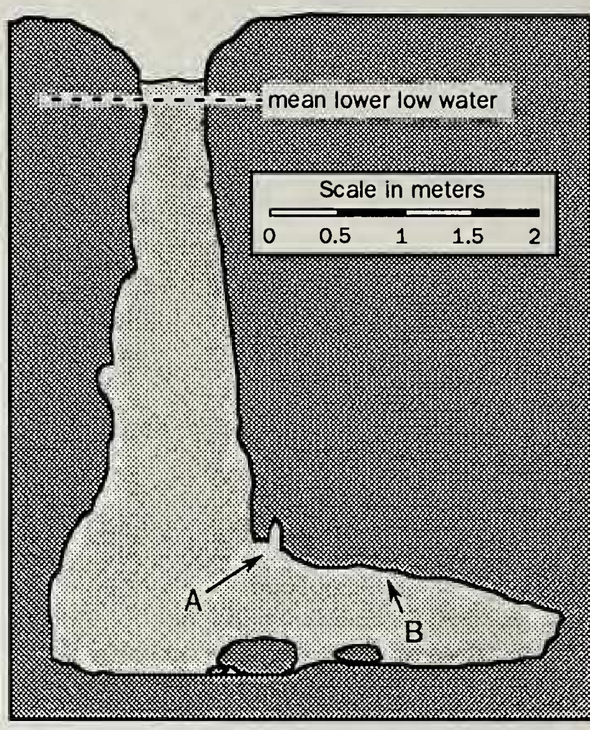

Figure 2

A schematic cross-section of the channel. A. The crack where the two largest air pockets occur. B. The overhang, which is often covered with small bubbles.

To confirm that the limpets remained stationary in the subtidal habitat, I selected three limpets that were completely out of the water in separate air pockets. A mark was made on the rock next to each limpet in line with a mark on the animal's shell, so that if the limpet changed location or orientation it would be apparent. One week later the limpets were rechecked.

RESULTS

Trapped beneath the ledge were a few dozen small bubbles (2.5 cm diameter, 10 mL volume), a few mid-sized bubbles (4 × 5 cm, 25 mL), and three large bubbles that averaged more than 250 mL (10 × 12 cm to 12 × 25 cm). The two largest bubbles were trapped in a deep crack on the edge of the overhang (Figure 2). Many small bubbles were observed along the underside of the ledge to its furthest recesses. The largest bubbles were not displaced about their periphery more than 1 cm by the surge, and the volume changes due to pressure differences between high and low tide were calculated to be less than 15%.

The results of the gas chromatography were inconclusive. The CO_2 levels of the bubbles were low—roughly between 0% and 0.5%—but at such levels, the method of measurement is imprecise. For comparison, atmospheric air contains approximately 0.035% CO_2, and a normal human exhalation contains 3–3.5%.

Tests in which pockets were emptied to observe the refill rate were unsuccessful because of an inability to return to the study site with sufficient frequency. On some occasions, pockets that had been emptied were found filled a week later; at other times pockets that had been full were found with less air in them. It was not possible to correlate these changes with other factors such as surf conditions, tidal levels, or the presence of divers. On one occasion, however, two sets of SCUBA divers passed next to the ledge shortly after a large pocket had been emptied. When both groups (a total of nine divers) had passed, the emptied pocket was rechecked, and the amount of air within it had not increased noticeably.

During one dive I noted that many of the limpets in a large pocket were attached several centimeters within the edge of the air bubble. Two weeks later the bubble was approximately half its previous size, and all of the limpets, including those formerly well within the edge of the bubble, were exposed to the water. The portion of rock that was still covered by air appeared completely barren. This seems to indicate a minimum size to the bubble that prevents any marine organism from settling.

Within the bubbles were found limpets (*Trimusculus reticulatus*), a few barnacles (*Balanus glandula*), and, on one occasion, a snail (*Ceratostoma nuttallii*). Spirorbid worms were frequently found on the backs of the limpets. In contrast, the areas immediately surrounding the pockets were inhabited by tube worms (*Serpulorbis* sp.) and sea urchins (both *Strongylocentrotus purpuratus* and *S. franciscanus*) and encrusted with various sponges.

Trimusculus was found in large numbers in pockets of all sizes. Bubbles with only 10 mL of air could contain as many as 4 or 5 limpets clustered together, a mid-sized pocket might contain 8, and the largest pocket had within it a colony of 61 limpets. Limpets collected ranged in size from 1.2 cm to 1.7 cm in diameter.

The limpets were found in tight aggregations, and the edges of their shells were often convoluted in close conformity with the irregular rock surface. One empty shell was attached firmly to the reef by a worm's tube. In the experiment in which marks were made on limpets and on the adjoining rock, all three limpets were found in the same position and orientation one week later.

DISCUSSION AND CONCLUSIONS

In an intertidal environment, *Trimusculus reticulatus* is exposed alternately to air, where it can breathe but not feed, and water, where it can feed. Because it does not graze, but "filter feeds" by secreting mucus (WALSBY, 1975), a limpet living in an air pocket must be exposed to the water at regular intervals. This study indicates that, in this subtidal environment, alternating periods of exposure to air and water are a result of natural changes in bubble size: there is no indication that subtidal *Trimusculus* deviates from the sedentary behavior reported for intertidal populations.

The results of this study suggest the following explanation for the origin of the air pockets. When the tide is sufficiently high (about +0.6 m, depending on the size of the surf), waves crashing over the rocks fill the water in the channel with tiny bubbles. The surge also brings in aerated water from the turbulent intersecting channel. As this air collects in the nooks of the ledge and in the deep cavities of the crack, the bubbles gradually grow. The bubbles diminish during low tides, when the current in the channel draws air from the large pockets. In some hollows, air may also seep slowly through the rock. The amount of air in the pockets changes gradually, however, remaining fairly constant over the short term.

YONGE (1958) suggested that the limpet's ability to breathe air may be the key to its survival in the face of intertidal competition. Similarly, in the subtidal habitat this trait allows *Trimusculus reticulatus* to take advantage of a refuge that is ostensibly quite different from the limpet's intertidal habitat. If nothing else, this unique situation reminds us to keep our eyes open for unexpected solutions to the demands placed on organisms by nature.

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